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WILLEY ON THE ENTEROPNEUSTA.

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DR. ARTHUR WILLEY has made such valuable contributions to our knowledge of the morphology of the lower Chordata that it is with high expectations one opens his recent memoir upon the Enteropneusta.¹ He describes in considerable detail many points in the anatomy of three species of *Ptychodera* (two of them new), of two species of *Spengelia* (one new), and of a *Tornaria*, all from the South Pacific, and also describes as new and distinct species belonging to the genus *Ptychodera* two West Indian forms, from Bimini (in the Bahamas) and from Jamaica. This anatomical part of the memoir is full of details of considerable interest to the student of the Enteropneusta, but hardly of such a nature as to permit description in this review. The author's observations, however, serve him as a foundation upon which to rest some very far-reaching theoretical conclusions, and to these it may be profitable to direct attention, referring to so much of the anatomy as may be necessary for a correct understanding of the basis for these conclusions.

Willey's first proposition is that "the gonads and gill slits were primarily unlimited in number and coextensive in distribution, the gonads having a zonary disposition and the gill slits occupying the interzonal depressions. The primary function of the gill slits was the oxygenation of the gonads, their secondary function being the respiration of the individual." In support of this contention that in the lower Chordata the series of gonads once extended much further forward, while the series of gill slits extended much further backward, the gill slits lying between the gonads and serving chiefly for their oxygenation,

¹ Willey, A. *Zoological Results*. Pt. iii, Enteropneusta from the South Pacific, with Notes on the West Indian Species. Cambridge, University Press, May, 1899.

the author urges (1) that in the Enteropneusta and Cephalochordata the number of gill slits is indefinite, new ones being added posteriorly throughout life; (2) that the number of gill slits has become reduced not only among the Vertebrata, but even within the group of the Enteropneusta, since one species, *Ptychodera auriantica*, has as many as seven hundred pairs, while another species, *P. mimeta*, never has more than forty pairs, these representing the two extremes so far as known; (3) that in the intestinal pores and ciliated grooves of certain Enteropneusta we have vestiges of the former posterior gill slits of the now abbreviated series. The intestinal pores occur in six species belonging to four genera. These pores may lie either close behind the branchial region or at the posterior end of the hepatic region. Schimkewitsch and Spengel have suggested that these pores may in some way be related to gill slits. In the Ptychoderidæ the pores are absent, but instead of them we have a pair of ciliated grooves extending from the anterior end of the hepatic region nearly to the posterior end of the body. In two species "these are not simple longitudinal furrows, but undergo metameric or interannular sacculations," the saccules "strongly resembling gill pouches" not yet open to the exterior. Willey believes that the restriction of the gill slits to the anterior part of the body and of the gonads to the middle portion of the trunk took place after the development of a blood vascular system, which rendered the gonads no longer directly dependent upon the gill slits for oxygenation.

Certain species of Enteropneusta have two proboscis canals connecting anteriorly with the proboscis cœlom and opening posteriorly by two pores on the dorsal side of the stalk of the proboscis, near where it joins the collar. The distal extremity of each of these canals may be swollen to form a considerable vesicle, or "end sac." Secondly, in some species one (or both?) of the proboscis canals may be interrupted, so that the end sac, while opening to the exterior, has no longer any communication with the proboscis cœlom. In certain adults, though not in the young, of one species, *Ptychodera carnosa*, Willey found that one of the two proboscis pores "may open" not onto the

posterior part of the dorsal surface of the proboscis stalk, as in other species, but "into the base of the medullary tube, somewhat behind the anterior neuropore."

"By a legitimate mental abstraction" Dr. Willey derives from this fact a "theory, as to the broad truth of which" he is himself "quite convinced," and which he states in these words: "The proboscis pore of the Enteropneusta is represented by and is homologous with the inner or cerebral opening of the neuro-hypophysial apparatus of the ascidian larva; the end sac of the Enteropneusta typically communicates internally with the coelom, but within the limits of the group we find signs of its emancipation from the coelom; the hypophysial canal of the ascidian larva has no relations with the body cavity, but it opens at one end into the medullary tube (cerebral vesicle) and at the other into the branchial sac at the base of the buccal cavity. Thus a special significance is given to the peculiar mode of origin of the ascidian subneural apparatus (gland and duct), and an explanation is forthcoming as to the apparent absence of anything like a proboscis pore in the ascidian larva." This adds another and startling hypothesis to the several that have been advanced as to the homologies of the ascidian neural gland. Allow me to refer for a moment to these.

Masterman's recent attempt to homologize the so-called notochordal pouch of the Hemichordata with the ascidian neural gland seems to imply a failure to understand the real nature of the latter organ. The notochordal pouch, so far as we can judge, is endodermal, a derivative of the pharynx. The neural gland of ascidians¹ is derived from the central nervous system, its duct is the anterior end of the central neural tube, and its aperture is usually regarded as the neuropore. The neural gland has no known relation to the endoderm, except that it opens into a portion of the pharynx which may be of endodermal origin, but which there is some reason to believe may be derived from the stomodæum.

¹ I say the neural gland of ascidians rather than of Tunicata, because the neural gland of certain tunicates, the Salpidæ, is of such a peculiar nature that it is difficult to compare it with that of the ascidians.

Wiley's attempt to homologize a portion of one or both of the proboscis canals¹ and their pores with the ascidian neural gland seems even a greater exercise of the imaginative faculty, for these structures in Ptychodera are not only mesodermal, but are a definite portion of the cœlom. If they be homologous with one or both of the collar pores and collar canals, as seems not improbable, then they must be regarded as nephridial in their relationships, for Masterman has clearly demonstrated the nephridial nature of the collar canals in *Cephalodiscus*. Wiley, however, does not claim that the proboscis canals and collar canals of Ptychodera have been derived from the ascidian neural gland, but rather that the gland in the ascidians has been modified from a more primitive condition similar to that in certain adult specimens of *Ptychodera carnosa*. How such a proposition can be reconciled with the facts of the development of the gland in the ascidians, where it is formed wholly at the expense of the larval neural canal, it is very difficult to see. Wiley's statement that the "hypophysial canal" of the ascidian larva "opens into the medullary tube" is hardly accurate. It is morphologically a part of the medullary tube. Dr. Wiley must have had these facts clearly in mind, for he has himself published one of the most valuable descriptions of the ontogenetic development of the ascidian neural gland.²

The whole question of the homologies of the neural gland of tunicates is an exceedingly complicated and difficult one. It is by no means certain even that this gland is represented in the vertebrates by either of the two portions of that compound structure which is called the hypophysis cerebri, yet this homology proposed by Julin is comparatively simple, since the ascidian gland and one part of the vertebrate hypophysis are of neural origin. Wiley's theory is much more startling, for it claims a genetic relationship between a portion of the central nervous system in ascidians (the neural gland) and a portion of the cœlom (the proboscis canals) in Enteropneusta. Yet the only foundation for the theory which I am able to find in his paper

¹ Wiley regards the condition with two proboscis pores as more primitive than that with one.

² Several further objections to the proposed homology might be urged, but it seems hardly wise to treat the theory too seriously.

is the fact that in certain adult individuals of one species of *Ptychodera* he finds sometimes one, sometimes the other, of the two proboscis pores opening "into the base of the medullary tube somewhat behind the anterior neuropore." In younger specimens he finds the single median proboscis pore opening somewhat in front of the "anterior neuropore." The occasional peculiarity he has observed in *Ptychodera carnosa* seems a rather narrow apex on which to found so broad a pyramid of theory.

Willey's third proposition as to regional pores and nephric tubules is best presented by copying his own table, which is self-interpreting, with the one explanation that the organs mentioned in the right-hand column are not intended to be represented as serially homologous with those in the preceding columns.

GROUP.	ARCHIMERIC SYSTEM.			ESSENTIAL ORGANS OF EXCRETION.
Ideal . . .	Protomeric pores	Mesomeric pores	Opisthomeric pores	Regional pore canals
Enteropneusta	Proboscis pores	Collar pores	Truncal pores (Spengelia)	Glomerulus
Cephalochorda	Præoral pit and Olfactory pit	Hatschek's nephridium	Lankester's brown funnels	Boveri's nephric tubules
Urochorda	Neuro-hypophysis (in part) ¹			{ Renal vesicles: Organ of Bojanus (Molgulidæ)
Vertebrata	Hypophysis (in part) ¹			{ Pronephros Mesonephros Metanephros

In some of the *Ptychoderidæ* Willey found that the collar nerve tube does not completely separate from the dorsal epidermis from which it arose, but that there are partially hollow connecting strands running from the nerve tube to the mid-dorsal line of the collar. The more or less interrupted lumina of these

¹ In part because cœlomic element is wanting.

hollow strands may in certain cases connect with the lumen of the central nerve tube. These hollow strands or "roots of the Ptychoderidæ," Willey says, "are genetically related to the epiphysal complex of Craniota; in the crucial nuchal region of the Enteropneusta are, therefore, to be found not the actual but the nearest possible approximation to the actual primordia of the . . . epiphysis cerebri of Craniota." Of course this *may be* true, yet it seems questionable if it be "profitable for doctrine."

Willey's fifth proposition he states as follows: "Just as the medullary tube of the collar is admittedly an invaginated portion of the dorsal nerve trunk,¹ so the medullary folds which arise and fuse to form the medullary tube are to be regarded as specializations of the anterior portion of the pleural folds which are retained in the Ptychoderidæ as the genital pleuræ." "The genital folds of Enteropneusta, the atrial folds of Amphioxus, and the medullary folds of Vertebrata belong to the system of pleural folds of the body wall, and are differentiated from a common primordium." In this connection it may be well to remember that Amphioxus has both medullary folds and atrial folds, and that there is no apparent relation between them.

Willey's sixth proposition refers to a recession of the "posterior neuropore" until it reaches and becomes associated with the blastopore ("primitive anus") to form the neurenteric canal. I do not, however, clearly understand the terms he uses.

Dr. Willey next discusses briefly the different regions of pseudo-chondroid tissue, *i.e.*, "stomochord, pygochord, and pleurochords."

Willey points out that the tongue bars of the gill region of the Enteropneusta "are not (ontogenetically) secondary, as they are in Amphioxus," and that "by their development, size, and

¹ Cf. Morgan (*Journal of Morphology*, vol. ix, 1894, p. 74). "We see in Balanoglossus that the *invaginated* dorsal nerve cord can correspond only to the anterior end of the nerve cord of Amphioxus, and that the *superficial* dorsal nerve path, stretching through the gill region, thence to the end of the body, must be the homologue of the remainder of the nerve cord of Amphioxus."

vascularity, they obviously constitute collectively the essential organs of respiration. In *Amphioxus* the functional importance of the tongue bars is greatly diminished; they are smaller in size and lower in vascularity than the primary bars, and their development is secondary."

In certain of the Enteropneusta the ventral edges of the gill slits are swollen on the pharyngeal surface, and these thickened areas of the walls of the successive gill slits are continuous, forming a pair of lateral ciliated pharyngeal ridges. These "arch round in front to unite in the epibranchial band," and represent the endostyle of *Amphioxus* and the Tunicata.

In one part of his memoir Dr. Willey describes certain phenomena of regeneration in *Ptychodera flava*, summarizing them as follows:

(1) "When regeneration occurs in the region of the genital pleuræ the collar is regenerated from the pleuræ.

(2) "The collar nerve tube is formed by the fusion of true medullary folds which are differentiated from the pleural folds.

(3) "The zones of the collar are differentiated from the annulations of the body wall.

(4) "In regenerating individuals the right and left proboscis pores are approximately equal.

(5) "In regenerating individuals the lumen of the stomochord¹ is at first entire."

I trust the absence of comment in this review upon some of the proposed theories will not be interpreted as indicating my acceptance of these theories. The paper is noteworthy for the boldness and confidence with which it sets forth startling propositions.

THE WOMAN'S COLLEGE OF BALTIMORE,
January 9, 1900.

¹ Notochord of Bateson.